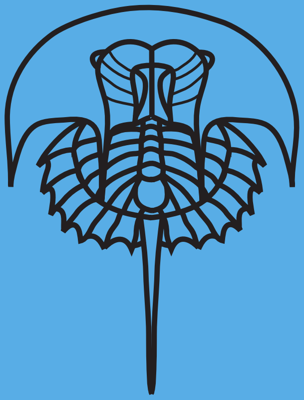

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PART N, REVISED, VOLUME 1, CHAPTER 16: ORIGIN AND EARLY EVOLUTION OF THE BIVALVIA

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CAMBRIAN ARCHETYPE (STEM-GROUP) BIVALVES

ORIGIN OF CAMBRIAN ARCHETYPE BIVALVES

Since the publication of the Bivalvia volumes of the *Treatise on Invertebrate Paleontology* in 1969 (Cox, Nuttall, & Trueman, 1969), with the exclusion of *Lamellodonta* Vogel, 1962, from the Bivalvia, and with dramatic increases in our knowledge of Cambrian and Ordovician bivalves and their close relatives, much progress has been made in our understanding the origin and early evolution of this class.

The Diasoma hypothesis of Runnegar and Pojeta (1974) has been overturned by evidence that the Scaphopoda and Cephalopoda are sister groups within Cyrtosoma (Waller, 1998; Haszprunar, 2000; Wanninger & Haszprunar, 2001; Giribet & Wheeler, 2002; Passamaneck, Schander, & Halanych, 2004; Giribet & others, 2006). Waller (1998) suggested the Stenothecidae-Rostroconchia-Bivalvia clade, which stands alone as monophyletic, diverged prior to the common ancestor of Gastropoda, Scaphopoda, and Cephalopoda.

Watsonella Grabau, 1900 (=*Heraultipegma* Pojeta & Runnegar, 1976) was once regarded as the earliest and most primitive rostroconch, as well as a direct link between stenothecid monoplacophorans and the Bivalvia (Runnegar & Pojeta, 1974, 1985; Pojeta & Runnegar, 1976, 1985; Kouchinsky, 1999, 2000). However, MacKinnon (1985) argued that *Watsonella* is not a rostroconch because it has no indication of pegma. Carter, Campbell, and Campbell (2000) also assigned *Watsonella* to Stenothecidae rather than to Rostroconchia. MacKinnon (1985) believed that bivalves are descended directly from monoplacophorans rather than via an ancestral rostroconch stem as the Pojeta-Runnegar model presumed. Runnegar (1996) agreed that *Watsonella* may be better regarded as a direct link between stenothecid monoplacophorans and the Bivalvia rather than the oldest known rostroconch. The phylogenetic analysis of Carter, Campbell, and Campbell (2000) suggested that the Bivalvia is more closely related to *Watsonella* (Stenothecidae) and *Pseudomyona* Runnegar, 1983 (Pseudomyonidae) than to *Anabarella* Vostokova, 1962, and the Rostroconchia. It seems that the Rostroconchia and Bivalvia share common laterally compressed pseudomyonid + stenothecid ancestry (MacKinnon, 1985; Carter, Campbell, & Campbell, 2000). The latter authors argued it is difficult to imagine how a hinged shell could have been derived from the specialized, rigidified dorsal area of pegma-bearing rostroconchs. Thus, the first evolutionary step from monoplacophorans toward both rostroconchs and bivalves was lateral compression of the shell, i.e., the Stenothecidae-Rostroconchia-Bivalvia clade diverging from monoplacophoran ancestors (event 1) in the early early Cambrian. That is to say, the Bivalvia is evolved directly from epifaunal, crawling, laterally compressed monoplacophorans. The transition from laterally compressed monoplacophoran to rostroconch involves the acquisition of a pegma and the pseudobivalved condition,

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whereas the transition from laterally compressed monoplacophoran to bivalve (event 2) involves the appearance of a true hinge, one or two adductor muscles, and differentiation of two lateral centers of calcification. All these directly led to the birth of the bivalve body plan and also the origin of Cambrian archetype bivalves (i.e., stem-group bivalves, =Euprotobranchia NEVESSKAJA, 2009). In summary, bivalves and rostroconchs represent two different evolutionary directions. The hypothesis that lateral compression of a yet uncalcified shell preceded the subsequent appearance of lateral centers of calcification (YONGE, 1978) is not supported by the fossil record (RUNNEGAR & POJETA, 1985). The establishment of the true bivalved condition was undoubtedly accompanied by the emergence of hinge teeth to guide the valves during closure and the formation of adductor muscles.

BANDEL (1988, fig. 8.5, 18) illustrated an aberrant embryonic shell of *Anodonta cygnea* with so-called monoplacophoran morphology, because it failed to form two centers of calcification. This example proved that bivalves did evolve from laterally compressed monoplacophorans. It is suggested that the evolution of the first bivalves with two centers of calcification from univalves is only a one-step alteration (BANDEL, 1988).

Homeobox genes are a group of related genes that specify the anterior-posterior axis and segment identity of metazoan organisms during early embryonic development and play pivotal roles in animal body plan formation (IIJIMA & others, 2006, and references therein). Each phylum or class exhibits a unique pattern of gene duplication or loss in the Hox cluster (VALENTINE, ERWIN, & JABLONSKI, 1996). Among Hox genes, the *engrailed* gene was first found in the fruit fly *Drosophila* to control segmentation, limb development, and nervous system development. Subsequently, it was found to have similar roles in other animals (GIBERT, 2002 & references therein; NEDERBRAGT, VAN LOON, & DICTUS, 2002, and references therein). A skeletogenetic function of *engrailed* genes that evolved at or near the base of the bilaterian clade may help explain the sudden appearance of shelly fossils during the Cambrian evolutionary explosion (JACOBS & others, 2000). On the other hand, the *decapentaplegic* (*dpp*) gene, initially isolated from the genome of *Drosophila melanogaster* MEIGEN, belongs to the transforming growth factor-β (TGF-β) family of secreted polypeptides and is involved in dorsoventral axis specification in both vertebrates and insects (NEDERBRAGT, VAN LOON, & DICTUS, 2002, and references therein). Recent studies have shown that the Hox genes *engrailed* (MOSHEL, LEVINE, & COLLIER, 1998; JACOBS & others, 2000; WANNINGER & HASZPRUNAR, 2001; BARATTE, ANDOUCHE, & BONNAUD, 2007) and *dpp* (NEDERBRAGT, VAN LOON, & DICTUS, 2002; IIJIMA & others, 2008; KIN, KAKOI, & WADA, 2009) are responsible for shell formation in gastropods, chitons, bivalves, scaphopods, and cephalopods. It is suggested that *engrailed* and *dpp* are involved in setting up a compartment boundary during shell development in mollusks (NEDERBRAGT, VAN LOON, & DICTUS, 2002; KIN, KAKOI, & WADA, 2009). Bivalve embryonic shell (prodissoconch I) formation starts with two centers of calcification (KNIPRATH, 1981; WALLER, 1981, 1998), both bearing *engrailed* expressing cells (JACOBS & others, 2000, fig. 3H), probably indicating a link between the separation of two centers of calcification and the regulation of *engrailed* expressing cells in embryonic shell formation. NEDERBRAGT, VAN LOON, and DICTUS (2002) concluded that *engrailed* became involved in shell formation because of its ancestral role, which is to set up compartment boundaries between embryonic domains. KIN, KAKOI, and WADA (2009) argued that the *dpp* homolog in the oyster *Saccostrea kegaki* TORIGOE & INABA, 1981, is expressed only in the cells along the dorsal midline and contributes to hinge structure formation in the Bivalvia, whereas the conserved role of *engrailed* is restricted to shell field formation. In any case, the available evidence argues in favor of a primary univalved (embryonic) shell as being plesiomorphic for Conchifera, whereas a secondary bivalved shell is apomorphic for Bivalvia (Wanninger & Haszprunar, 2001).

Carter, Campbell, and Campbell (2000) suggested that the evolutionary transition from stenothecid monoplacophoran to true bivalve required microstructural differentiation of the ligament, the evolution of at least one adductor muscle, loss of permanent shell gapes, and rearrangement of imbricated, matted/lamello-fibrillar laminae into imbricated, nacreous laminae as in fordilloids, or imbricated, calcitic, foliated laminae as in tuarangioids. As is well known, the lower and middle Cambrian genera *Fordilla* Barrande, 1881, and *Pojetaia* Jell, 1980, had basically completed this transition and possessed the above-mentioned body plan; therefore, they are acknowledged as being the earliest true bivalves. Some scholars have doubted whether middle Cambrian *Tuarangia* MacKinnon, 1982, is a bivalve (Runnegar & Pojeta, 1992; Pojeta, 2001), but it does have closer affinity with Bivalvia than with *Pseudomyona,* because *Tuarangia gravgaerdensis tenuiumbonata* Hinz-Schallreuter, 1995, shows short, anterior and posterior pseudoligament insertion areas, differentiated left and right beaks, and possible anterior and posterior adductor muscle scars (Carter, Campbell, & Campbell, 2000). The immediate common ancestor of Tuarangiidae and Fordillidae probably had a divided larval shell and a pseudoligament as Carter, Campbell, and Campbell (2000) suggested. *Tuarangia* should be considered one of the stem groups of the Bivalvia (Carter, Campbell, & Campbell, 2000), although it has nothing to do with the true Pteriomorphia (Fang, 2006c). The evolution of calcitic foliated shell fabric in *Tuarangia* is clearly convergent with later pteriomorphians.

Waller (1990, 1998) indicated that the primitive bivalve ligament was a three-layered structure (periostracum, lamellar sublayer, fibrous aragonite sublayer); the latter two are not continuous with shell layers and probably originated as repair material secreted as a response to continued flexure and fracturing at the posterodorsal part of the shell. The anterior adductor may have originated by cross-fusion of radial muscles along the dorsal side of the anterior mantle embayment, but the posterior adductor resulted from cross-fusion of radial mantle muscles in a more ventral position, below the rectum (Waller, 1998).

The Bivalvia is characterized by the virtual absence of a head and associated sensory structures. This contrasts sharply with the complex head anatomy of active nektonic cephalopods and many other invertebrates. The reduction or loss of the head and associated structures, such as the radula, is consistent with the appearance of lateral compression of the pseudomyonid + stenothecid ancestors of the Bivalvia, which elevated the head relative to the crawling surface of the foot, and which, therefore, elevated the mouth and radula above the substratum (Yonge, 1939, p. 133). Waller (1998, p. 8) suggested that “head reduction” and “radular reduction” had probably already occurred in ancestral stenothecids, as well as rostroconchs, based on the absence of radular muscle attachment scars.

The acquisition of hinged shell valves in Cambrian archetype bivalves inevitably resulted in their further reduction. The bivalve body was enclosed completely by a calcareous shell composed of two valves, and its head and associated structures were out of direct contact with the external environment. The evolution of labial palps, which are uniquely bivalvian structures and which differ from the oral structures of other molluscan classes, is a logical consequence of this change in body organization (Waller, 1998). As independent food-gathering organs, the initial palps probably received food from the foot. That is, stem-group bivalves must have used pedal-palp feeding with a ventrally emergent foot, since there is as yet no evidence for trophic differentiation between filter-feeding and deposit-feeding among Cambrian archetype bivalves (FANG, 2006a).

LIFE HABITS OF CAMBRIAN ARCHETYPE BIVALVES

The Cambrian archetype bivalves *Fordilla, Pojetaia,* and *Tuarangia* are stem-group taxa that predate the latest common ancestor of the crown-group Bivalvia (MORRIS, 1990; WALLER, 1990, 1998; RUNNEGAR & POJETA, 1992; CARTER, CAMPBELL, & CAMPBELL, 2000; FANG, 2006a). Both *Fordilla* and *Pojetaia* possess a bivalved shell, a simple, opisthodetic pseudoligament, simple dentition (pretaxodont, *sensu* CARTER, CAMPBELL, & CAMPBELL, 2000; CARTER, 2001), and a series of very well-impressed muscle scars, the number and size of which are variable (GEYER & STRENG, 1998). These muscle scars are approximately in the position of the adductor and pallial line muscle scars of many living bivalves, but they are otherwise rather dissimilar (MORRIS, 1990). *Fordilla* has an unusually large set of muscle insertions forming the posterior part of its pallial line (POJETA & RUNNEGAR, 1976). STANLEY (1975b, 1977) indicated that *Fordilla* displays unusual and problematical muscle scars in the region of pedal emergence, and that the morphology and function of these muscles are uncertain. Therefore, these primitive bivalves are assumed to have retained a plesiomorphically ventrally emergent foot, rather than an anteriorly emergent one, as in post-Cambrian bivalves. Although *Pojetaia* had a small anterior adductor scar, RUNNEGAR and BENTLEY (1983) emphasized the possibility that the pallial muscles in this position may not yet have been cross fused. In brief, the organs of *Pojetaia* and *Fordilla* are still at an incipient bivalve evolutionary stage (FANG, 2006a).

The interpretation of infaunal habits for Cambrian bivalves has long been influenced by an actualistic approach, which assumes that early bivalve evolution can be inferred from its crown group (FANG, 2006a). However, the Cambrian was not just a time of transition from matgrounds to mixgrounds but also a transition from cohesive, fine-grained sediments to softer, soupier substrates, characteristic of the rest of the Phanerozoic (SEILACHER, 1999; BOTTJER, HAGADORN, & DORNBOS, 2000; DORNBOS, BOTTJER, & CHEN, 2004; SEILACHER, BUATOIS, & MÀNGANO, 2005; CARON & others, 2006). Thus, the paleoecological model for pre-Ordovician archetype bivalves and paleoenvironments is, to a large extent, distinct from modern marine benthic environments. Consequently, the early evolution of archetype bivalves must have been accomplished on matgrounds, the cradle for the early evolution of metazoans (FANG, 2006a).

Contrary to common assumptions, the advent of a laterally compressed shell is not necessarily synchronous with the advent of pedal burrowing. First of all, the animal must have accomplished the transition from a primitive, flat, creeping foot to a highly extensible, muscular hydraulic foot when the transition was made toward active burrowing. Burrowing requires a great deal of movement of shell and foot, meaning that the two valves must be interlocked with teeth and sockets, and that muscle fibers should be firmly affixed to the shell. It also requires a true ligament, i.e., one with microstructurally differentiated outer tensional and inner compressional sublayers, to assist in opening the valves. Moreover, burrowing into soft substrates consists of repeated adduction and opening of the valves in the forward and backward rotational movements, integrated with protraction and retraction of the foot. This, in turn, requires a complex integration of the muscular system (TRUEMAN, 1966; STANLEY, 1970, 1975b; POJETA, 1987). *Fordilla* and *Pojetaia* are not very similar to most Ordovician burrowing protobranchs in shell shape and inferred musculature (FANG, 2006a). The failure of Cambrian bivalves to diversify greatly suggests that they had not yet crossed an adaptive threshold in terms of body size and/or complexity (STANLEY, 1975b), and that this adaptive threshold for infaunal life was not crossed until the Ordovician (FANG, 2006a). This situation is analogous to lingulid brachiopods, which similarly did not become infaunal burrowers until the Ordovician (Wright, 1979; Ushatinskaya, 2001; Harper & others, 2004; Zhang & others, 2005).

Ontogenetic studies can provide a basis for identifying plesiomorphic features and inferring early evolution, because ontogenetic trajectory contains phylogenetic information, although in an imprecise way (Arthur, 2002). In the Bivalvia, the early settled spat usually has the tip of its foot flattened and a predominantly anterior feeding and respiratory current. This is arguably the most economic current system suited for epibenthic creeping habits on firm substrates, and it has therefore been regarded as plesiomorphic for both protobranchs and autobranchs (Yonge, 1939; Allen, 1978, 1985). Such a current is found in all bivalves for at least a short period during early post-metamorphic development (Stasek, 1963; Allen, 1985; Reid & others, 1992; Waller, 1998), and it probably also occurred in Cambrian archetype bivalves (Fang, 2006a). These features have suggested to malacologists that the earliest bivalves were small surface-dwellers with labial palp-pedal feeding, moving over organically rich matgrounds in an upright stance, similar to many living leptonids (Allen, 1985; Morton, 1995). The ventrally emergent foot is used both to move and feed, and the gills function only in respiration. Reid and others (1992) pointed out that labial palp-pedal feeding may be a ubiquitous and primitive mechanism of food capture in all post-larval bivalves, including Protobranchia and Autobranchia. This conclusion has become widely accepted (Yeager, Cherry, & Neves, 1994; Morton, 1995; Gatenby, Parker, & Neves, 1997; Waller, 1998; O'Beirn, Neves, & Steg, 1998; Chaparro, Videla, & Thompson, 2001; Veniot, Bricelj, & Beninger, 2003).

Feeding in crown-group bivalves entails a pair of labial palps on each side of the mouth. These either transport food from the gills to the mouth, in Autobranchia (the labial palp-ctenidia filter feeding mechanism), or, with the addition of distally placed palp proboscides, they carry organically rich sediment directly to the mouth, as in Protobranchia (the labial palp-palp proboscides deposit feeding mechanism) (Morris, 1979). Therefore, gill-touching palps are the necessary requirement for the development of the additional feeding function of the gills, and filter feeding cannot have started until the palps came into contact with the gills (Morris, 1979; Vogel & Gutmann, 1980). The palps may have been preadapted for carrying food from the gills to the mouth (Fang, 2006a). The interpretation that deposit feeding via palp proboscides was the initial mode of feeding in the Bivalvia (Yonge, 1939, 1983) is no longer widely accepted (Stasek, 1961; Allen, 1985; Reid & Brand, 1986; Levinton, Ward, & Thompson, 1996; Waller, 1998; Stead, Thompson, & Jaramillo, 2003). Proboscides-palp deposit feeding was developed only in Protobranchia, and it should be regarded as a nuculoid specialization (Morton, 1995). Runnegar and Bentley (1983) suggested that *Pojetaia* and *Fordilla* were anatomically like a young *Nucula*; but in Fang's (2006a) opinion, they were at a proto-palpal evolutionary stage. In any case, it is improper to place *Pojetaia* and *Fordilla* in Nuculoida (Protobranchia) (Runnegar & Pojeta, 1992; Cope, 1997; Geyer & Streng, 1998; Cope & Babin, 1999; Hinz-Schallreuter, 2000), because they probably lacked palp proboscides, which are unique to Protobranchia (Waller, 1998), as well as paleotaxodont hinge teeth, which are characteristic of the earliest Protobranchia (Carter, Campbell, & Campbell, 2000).

Regarding the ctenidial-labial palp junction, Stasek (1963) regarded as primitive his Category I, wherein the gills remain unfused to the palps. However, the development of the gills in post-settlement individuals of the scallop *Placopecten magellanicus* (Gmelin, 1791) (Veniot, Bricelj, & Beninger, 2003) confirm Waller's (1998) opinion that the more primitive state is no contact at all between palps and gills. The cilia on the foot of the spat can transport food particles to the labial palps (Chaparro, Videla, & Thompson, 2001). Yeager, Cherry, and Neves (1994) documented the transition from pedal-palp feeding to gill-palp filter feeding in juvenile rainbow mussels, *Villosa iris* Lea, 1829 (Unionidae). Pedal-palp feeding is the major method of obtaining nutrients in the proto-palpal stage of protobranch juveniles, before the transition to proboscides-palp deposit feeding (Morton, 1995). The fact that in early postlarval bivalves the palps receive food particles directly from the ciliary tracts of the foot, or from a pedally induced anterior current (Reid & Brand, 1986; Reid & others, 1992; Morton, 1995; Waller, 1998; Chaparro, Videla, & Thompson, 2001; Veniot, Bricelj, & Beninger, 2003), suggests that the earliest bivalves were pedal-palp feeders, and that neither gill-palp filter feeding (Stasek, 1961, 1965; Stanley, 1975b; Tevesz & McCall, 1976, 1985; Vogel & Gutmann, 1980) nor labial palp-palp proboscides deposit feeding (Yonge, 1939; Purchon, 1978; Morris, 1979, 1980) is the primordial feeding mechanism in Bivalvia. Therefore, the basal dichotomy of subclasses Protobranchia and Autobranchia did not occur before the late Cambrian (Fang, 2006a).

The earliest mollusks are presumed to have crawled over microbial mat–bound seafloors and grazed the sediment surface for microbes (cyanobacteria) and organic particles (Salvini-Plawen, 1985; Seilacher, 1999; Bottjer, Hagadorn, & Dornbos, 2000; Seilacher, Buatois, & Màngano, 2005; Caron & others, 2006). This includes Cambrian archetype bivalves (Fang, 2006a), which inherited epibenthic gliding-creeping habits from the molluscan archetype (Salvini-Plawen, 1985). In summary, Cambrian archetype bivalves were surface-dwelling animals, epifaunal and/or interstitial crawling, moving and feeding on the top few millimeters of microbial mats, stuffing food into their mouth by means of ciliary currents on a ventrally emergent foot (Fang, 2006a). As Morton (1995) pointed out, they used the foot both to move and to feed, and their gills remained small and simple, functioning only for respiration.

LATE CAMBRIAN CRISIS (EVENT 3) AND THE ORIGIN OF CROWN-GROUP BIVALVES (EVENT 4)

Stanley (1975a, 1977) suggested that the earliest bivalves were only marginally successful. No adaptive radiation occurred among archetype bivalves, which remained at low diversity from the time of their appearance in the early Cambrian through the end of the Cambrian (Fang, 2006a).

The failure of Cambrian bivalves to diversify is probably related to the Cambrian change from Neoproterozoic-style, coherent matgrounds to Phanerozoic-style, soupier mixgrounds. This exposed Cambrian archetype bivalves to new environments for which they were not yet anatomically well adapted. As suggested by Fang (2006a), when archetype bivalves entered infaunal habitats and began crawling on and in soft, fine sediment, their simple gills were easily clogged by their anterior inhalant current. They faced the adaptive challenge of keeping the gills and mantle cavity free of unwanted sediment. Most archetype bivalves did not respond well to this evolutionary challenge and went extinct. However, a few of them survived this evolutionary bottleneck by evolving pedal burrowing and more complex ciliary mechanisms involving lateral, frontal, and laterofrontal cilia (Morton, 1995). Laterofrontal cilia are unique to Bivalvia and are present in both subclasses (Waller, 1998). Lateral cilia create the ventilating current, whereas the longer laterofrontal cilia stop particles and pass them to frontal cilia for acceptance as potential food or rejection and expulsion from the mantle cavity. Cilia lining the mantle cavity, foot, and gills sweep rejected sediment to the mantle edge, where it accumulates. Every now and then, the valves contract rapidly and flush these sediments out as pseudofeces. Most advanced bivalves evolved an additional strategy for avoiding sediment-clogging: they moved their inhalant current to the posterior end of the body, thereby leading to enlargement of the posterior end of the shell.

The latest common ancestor of modern-type bivalves (i.e., crown-group bivalves, =Eubivalvia CARTER, 2011) corresponds with branching point III of WALLER (1990, fig. 2). This ancestor originated from a founder population that had completed its genetic revolution and rapid morphological reorganization *sensu* MAYR (1942, 1954, 1963, 1982a, 1982b), somewhere in late Cambrian, Gondwanan shelf seas. Only when these modern-type bivalves became widespread, in the earliest Ordovician, did they become part of the known fossil record (FANG, 2006a).

FANG (2006a) suggested that Cambrian archetype bivalves almost disappeared during the late Cambrian so-called Dark Ages, based on the observations that (1) no Cambrian bivalve genus or species survived into the Ordovician; (2) no unequivocal bivalve fossils are known from the upper Cambrian (HINZ-SCHALLREUTER, 2000; COPE, 2002), a real fossil gap (RUNNEGAR, 1983; POJETA & RUNNEGAR, 1985) that constitutes a unique lacuna in the otherwise excellent fossil record of this class (BUDD & JENSEN, 2000); and (3) all early Ordovician bivalves are geographically restricted to the Gondwanan and peri-Gondwanan shelves. From the Tremadoc, earliest Ordovician onward, bivalves have a continuous fossil record. Geographic restriction and small population sizes may explain the gap in the fossil record between the latest known, middle Cambrian archetype bivalves and the earliest known, early Ordovician crown-group bivalves (FANG, 2006a).

When Cambrian archetype bivalves first entered infaunal habitats, they could use their foot and anterior inhalant current to feed (MORTON, 1995). The feeding gill may have initially evolved for increased respiratory efficiency in bivalves immured in sediments with no proficient connection with the water above, and with a need to clean the mantle cavity (MORTON, 1995). Once the gill-palp connection was established, filter feeding became an inevitable outcome (FANG, 2006a). COPE (1995, 1997, 2002, 2004) and COPE and BABIN (1999) correlated the evolution of the feeding gill with the explosive diversification of early Ordovician bivalves.

As suggested by ALLEN (1985), an elongate hindgut was established early in bivalve evolution, as shown by casts of a complex gut in a number of Ordovician nuculoids. This enabled the animal to ingest a large amount of inorganic sediment along with a small admixture of digestible food. These observations allow us to infer that Ordovician protobranchs possessed large labial palps, palp proboscides, and relatively small gills primarily involved in respiration. The array of shell forms displayed by Ordovician protobranchs is scarcely different in extent and composition from Recent protobranchs (ALLEN & HANNAH, 1986). There is overall similarity of arrangement of the mantle cavity and position of the muscle scars between Ordovician Praenuculidae and living Nuculidae (MORRIS & FORTEY, 1976; MORRIS, 1979).

The presence of a byssus in the young and/or adult stages of virtually all Pteriomorphia and Heteroconchia suggests that this feature evolved before these two subdivisions of Autobranchia separated. This points to a pre-Ordovician common ancestor possessing a byssus, at least in its larval stage. True byssal secretion is primitively absent in Protobranchia (ALLEN & HANNAH, 1986; BANDEL, 1988; MORTON, 1995) and is therefore an apomorphy for autobranchs but not for the entire Bivalvia (WALLER, 1998). The evolution of a byssus was an adaptive breakthrough of particular significance (STANLEY, 1972, 1977; MORTON, 1995). STANLEY (1975b) suggested that byssal attachment was a key feature for the origin and elaboration of sessile modes of life and for diversification among Ordovician endobyssate taxa. The secretion of byssus threads by a special gland at the base of the foot provided an effective means of attachment to hard surfaces and enabled autobranchs to secondarily return to epifaunal habitats, independent of the soft sediments inhabited by their infaunal ancestors.

The hypothesis of a small, geographically restricted, late Cambrian, Gondwanan founder population for modern-type bivalves is appealing, because it provides a plausible explanation for the late Cambrian gap in the known fossil record, the delayed adaptive radiation of the Bivalvia, and the evolutionary paleoecology of Cambrian and Ordovician benthos-substrate relationships (Fang, 2006a, 2006b).

ORDOVICIAN RADIATION OF CROWN-GROUP BIVALVES

It has long been acknowledged that the Ordovician is characterized by two diversification peaks, one in the early Ordovician and another in the late Ordovician (e.g., Babin, 1993, 1995, 2001; Cope & Babin, 1999; Cope, 2002, 2004). The first one is recorded mainly on the clastic platforms of northwestern Gondwana and peripheral microplates, whereas the second one is recorded mainly in carbonate and mixed platforms located at mid- to low-paleolatitudes in Laurentia, Baltica, Siberia, and Kazakhstan.

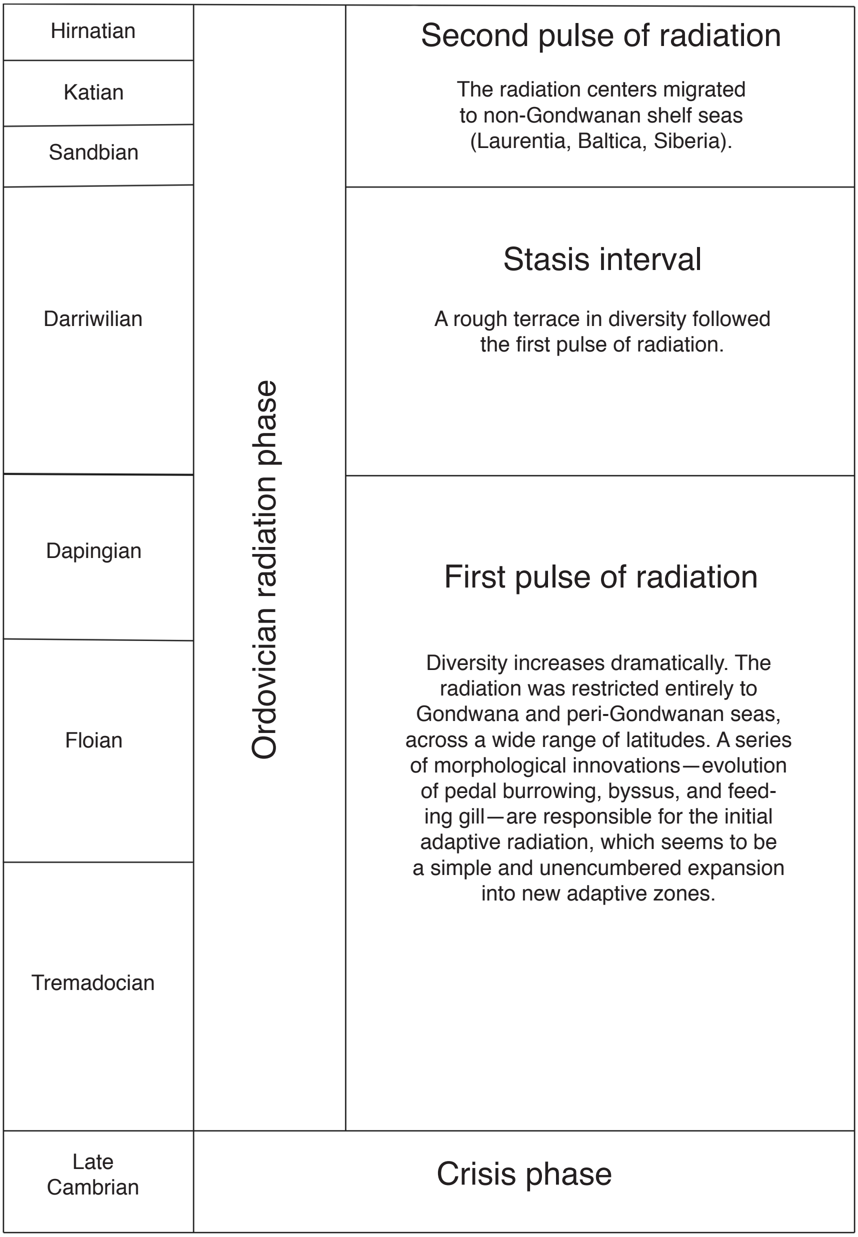
Fang (2006a) outlined the major evolutionary phases of bivalves during the Cambrian and Ordovician (Fig. 1). The Ordovician radiation began after a late Cambrian crisis and was characterized by an initial radiation event, an intermediate interval of stasis, and a second radiation event, terminating in the late Ordovician by global extinction. Sánchez (2007) described similar evolutionary stages and ecological transitions among Ordovician bivalves. As in other invertebrate taxa, the Ordovician was the most important time for appearance of new adaptive strategies in the Bivalvia.

EARLY ORDOVICIAN RADIATION

Since the classic works by Babin (1993, 1995), new discoveries have significantly increased our knowledge of Ordovician bivalves and have confirmed the key role of Gondwanan and peri-Gondwanan clastic shelves in the early evolutionary radiation. This paleogeographical area includes the late Tremadocian and early Floian carbonate platforms of the Precordillera of western Argentina, because this is believed to be an allochthonous terrain rifted from Laurentia in the late Cambrian and placed close to the proto-Andean margin by Floian time (Benedetto & others, 1999; Benedetto, 2004). Consequently, for most of the Ordovician, it was a peri-Gondwanan terrain, like Avalonia, South China, and other microplates (Fig. 2).

There are no known Ordovician survivors of Cambrian bivalve genera (Fang, 2006a). Rather, a new set of genera appeared, confirming that bivalves were affected by the extinction events of the Cambrian (cf. Zhuravlev, 2001). It is likely that the Ordovician bivalve clades originated from small isolated refugia of Cambrian populations in cold to temperate waters of Gondwanan and peri-Gondwanan regions. This would account for the fact that most of the oldest Ordovician bivalves are found along Gondwanan margins and not elsewhere (Cope, 1997; Cope & Babin, 1999; Sánchez, 2003; Fang, 2006a, 2006c). As Fang (2006a) stated, early Ordovician bivalves could have diversified from a founder population surviving the Cambrian biotic crisis, during which time the dichotomy between protobranchs and autobranchs was accomplished. The early Ordovician also saw the biogeographic divergence between bivalves inhabiting warm carbonate platforms and those inhabiting cold to temperate siliciclastic platforms.

Lower Tremadocian strata from northwestern Argentina (NWA) have yielded some presently unidentified bivalves that are larger (about 20 mm long) than bivalves recovered from upper Tremadocian strata. The latter bivalves are separated by a time of about 5 m.y. from subsequent Floian faunas, making the origination of many higher taxa in the Bivalvia appear to be more simultaneous than it may actually have been.



The radiation centers migrated to non-Gondwanan shelf seas (Laurentia, Baltica, Siberia).

A rough terrace in diversity followed the first pulse of radiation.

Diversity increases dramatically. The radiation was restricted entirely to Gondwana and peri-Gondwanan seas, across a wide range of latitudes. A series of morphological innovations—evolution of pedal burrowing, byssus, and feeding gill—are responsible for the initial adaptive radiation, which seems to be a simple and unencumbered expansion into new adaptive zones.

Fig. 1. Evolutionary phases of bivalves during the Ordovician (adapted from Fang, 2006a).

Most of the earliest Ordovician bivalves come from muddy sediments, allowing one to postulate that this kind of substrate favored diversification (Miller, 1988; Novack-Gottshall & Miller, 2003). However, early Ordovician bivalves were not confined to fine-grained, siliciclastic facies. For instance, some rare forms in the Precordillera are present in subtidal, upper Tremadocian to Floian limestones. Because these strata contain a rich fauna of gastropods, nautiloids, and rostroconchs,

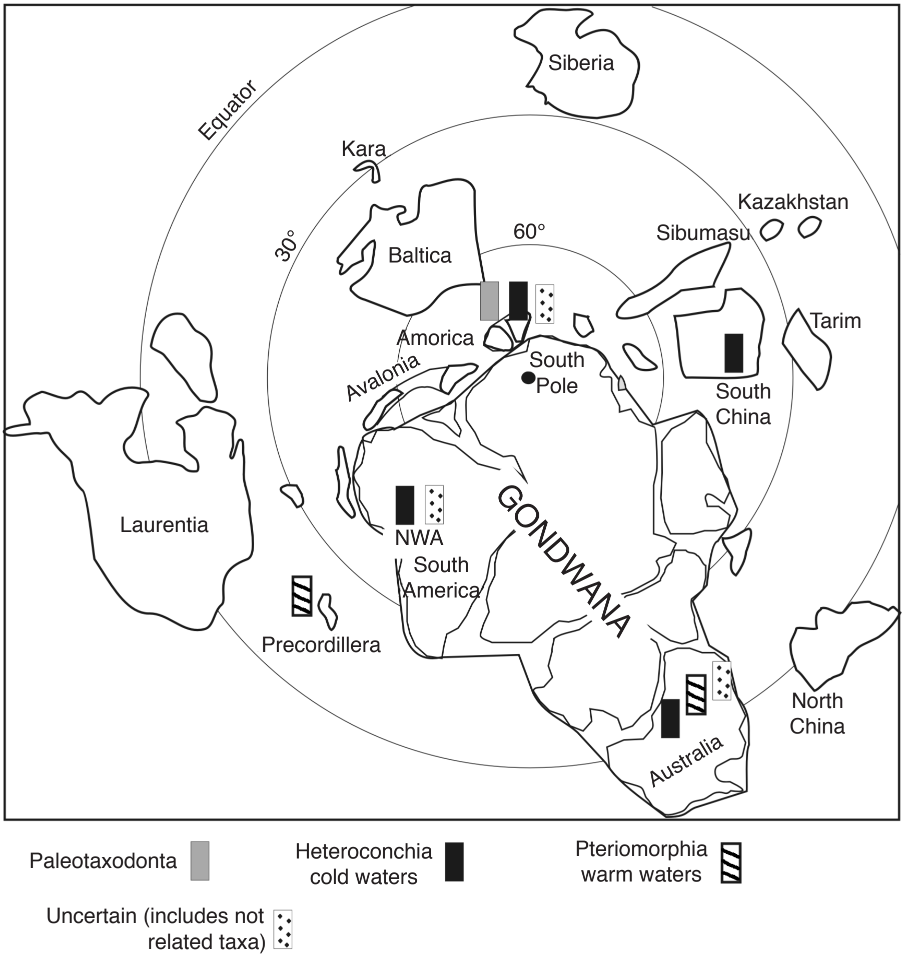


Fig. 2. Paleogeographic reconstruction of early Ordovician showing distribution of higher bivalve taxa; *NWA,* northwestern Argentina (paleogeographic map adapted from Benedetto, 2003).

the scarcity of bivalves is not a reflection of poor preservation. Novack-Gottshall and Miller (2003) suggested that most lower Ordovician bivalves proliferated in deep water sediments. However, this hypothesis has yet to be supported by sedimentological studies of Tremadocian-Floian localities, and in northwestern Argentina, the bivalve faunas represent inner platform settings (Astini, 2003, and references therein).

The oldest records of Ordovician bivalves, of Tremadocian age (Fig. 2), are confined to the NWA basin (Sánchez, 2008), the Montagne Noire of France (Babin, 1982), Australia (Pojeta & Gilbert-Tomlinson, 1977), and South China (Hsu & Ma, 1948; Fang, 2006a). Unidentified Tremadocian bivalves from the Moroccan Anti-Atlas were mentioned by Cope (2004).

The upper lower Tremadocian of the NWA basin has yielded *Losella* Sánchez, 2006, and *Goniophorina* Isberg, 1934, both taxa included in Modiolopsidae. The upper Tremadocian of NWA basin has yielded *Eoredonia* Sánchez, 2008; *Intihuarella* Sánchez, 2003 (in Sánchez & Vaccari, 2003); *Cienagomya* Sánchez, 2005; *Coxiconchia* Babin, 1966; *Ucumaris* Sánchez (in Sánchez & Vaccari, 2003);*Ucumaropsis* Sánchez, 2005; and *Lipanella* Sánchez, 2005

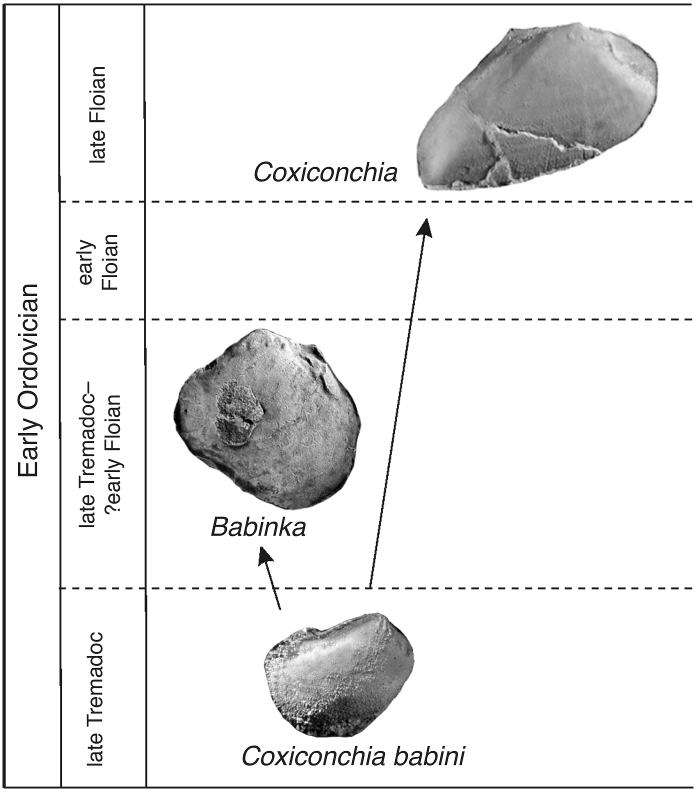


FIG. 3. Possible phylogenetic relationships of some Babinkidae (adapted from Sánchez, 2008).

(SÁNCHEZ, 2008). *Babinka* BARRANDE, 1881; *Noradonta* POJETA & GILBERT-TOMLINSON, 1977; *Ekaterodonta* BABIN, 1982; *Redonia* ROUAULT, 1851; *Synek* BARRANDE, 1881; and *Miquelana* BABIN, 1982, occur in the upper Tremadocian of the Montaigne Noire (BABIN, 1982). The upper Tremadocian fauna from the Pacoota Formation of Australia (POJETA & GILBERT-TOMLINSON, 1977) includes *Colpantyx* POJETA & GILBERT-TOMLINSON, 1977; *Pharcidoconcha* POJETA & GILBERT-TOMLINSON, 1977; *Xestoconcha* POJETA & GILBERT-TOMLINSON, 1977; *Cyrtodontula* TOMLIN, 1931; and *Deceptrix*? FUCHS, 1919. Since the Australian material is very scarce and lacks well-preserved hinges, assignation of *Deceptrix*? sp. to Protobranchia is uncertain. The Chinese material includes the single genus and species *Pharcidoconcha parallela* (HSU, 1948) (HSU in HSU & MA, 1948; FANG, 2006a).

The Precordillera terrain of Argentina contains *Modiolopsis*? HALL, 1847, upper Tremadoc, and a poorly preserved ambonychiid of lower Floian age, the earliest presently known member of its family (SÁNCHEZ, 2001).

The taxonomic composition of these assemblages indicates that Protobranchia, Pteriomorphia, and Heteroconchia differentiated at least as early as the early Ordovician. The heteroconch subgroup Anomalodesmata, the paraphyletic rootstock for infrasubcohort Cardiidia, was also distinct by this time, as shown by *Ucumaris* and *Ucumaropsis* (SÁNCHEZ & VACCARI, 2003). The relationships of some of the early Ordovician genera, such as *Synek*, remain uncertain (BABIN, 1982). This may be because some of the early Ordovician lineages originated in isolation, leading to the appearance of some lineages (e.g.,

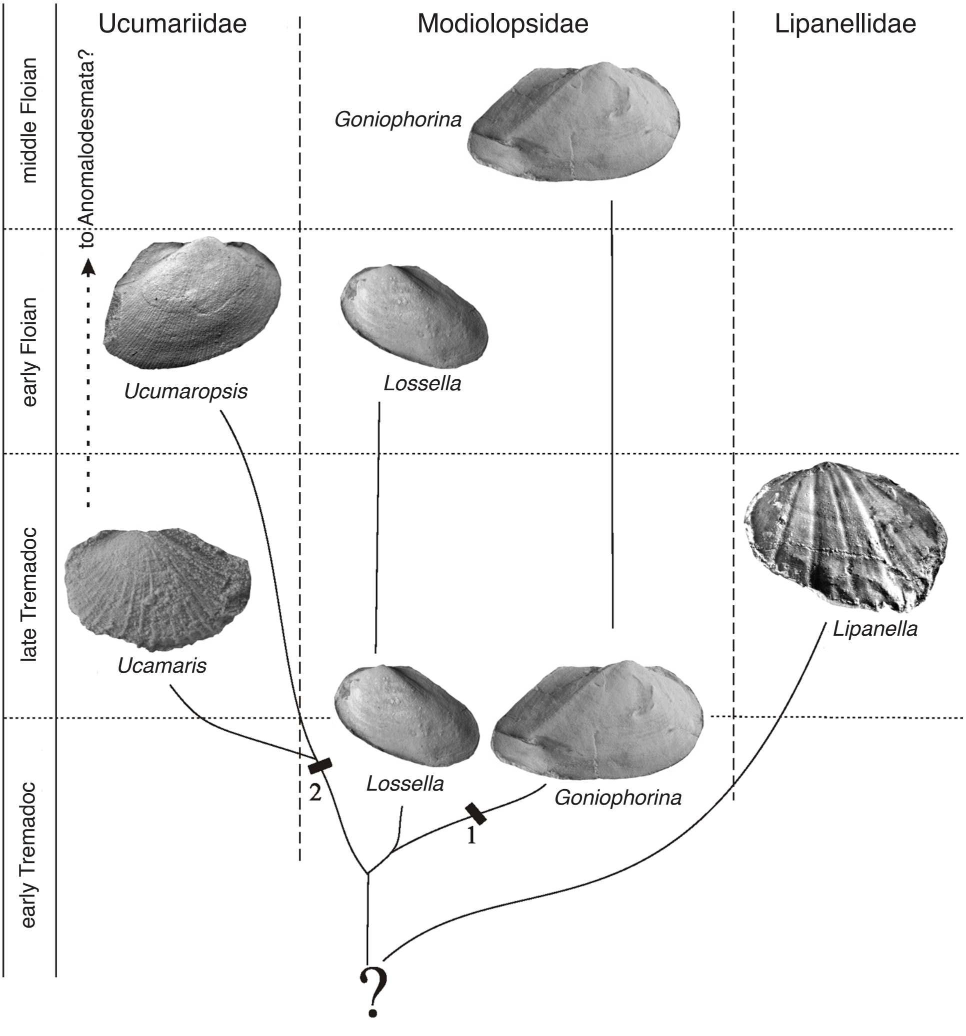


FIG. 4. Possible phylogenetic relationships between Goniophorinidae, Ucumariidae and Lipanellidae during the Early Ordovican; 1, carina; 2, pustules (adapted from Sánchez, 2006).

ucumarids, redoniids) that are ancestral to groups persisting through the Ordovician, as well as other lineages that are temporally and geographically restricted (lipanellids) and lineages that cannot be included within any modern higher taxon. Lipanellidae is presently placed in Heteroconchia as a near basal family, due to the presence of multiple subumbonal muscle scars.

Redoniids appear to have originated in northwestern Argentina, with *Eoredonia* SÁNCHEZ representing the base of their clade (SÁNCHEZ, 2008). *Coxiconchia babini* SÁNCHEZ, 2005, is a basal babinkid, which includes the coxiconchins (Fig. 3), and the intihuarellids *Intihuarella* SÁNCHEZ and *Cienagomya* SÁNCHEZ are basal cycloconchids (SÁNCHEZ, 2008). It seems likely that the ucumarids *Ucumaropsis* SÁNCHEZ, *Ucumaris* SÁNCHEZ, and *Arenigomya* COPE (1996) gave rise to the Anomalodesmata (COPE, 1996; SÁNCHEZ & VACCARI, 2003). Mineralized periostracal pustules of ucumarids favor placement of this family in Pholadomyoidea, but it could be related to the modiolopsids and probably also lipanellids (Fig. 4), forming a lineage characterized by an edentulous hinge, slopes at both sides of the umbo, and radial ornament (SÁNCHEZ, 2006). Alternatively, if ucumarids (and *Arenigomya*) did not give rise to the Anomalodesmata, they may represent a dead-end group that cannot be accommodated within current higher taxa. The main problem with early bivalve phylogeny is that the most basal forms for many higher taxa remain unknown. The earliest known early Ordovician heteroconchs and pteriomorphians already possess the synapomorphies characteristic of their group.

Beginning in the mid-Floian, and especially during the Dapingian, the number of bivalve genera increased exponentially in South Wales, Iberia, Australia, South China, Indochina, and Argentina. The scarcity of bivalves of this age in Bolivia may be due to lack of intensive searching. Some taxa are shared by several localities (e.g., *Babinka*, *Noradonta*, *Redonia*), but other taxa are very restricted geographically, such as *Catamarcaia* SÁNCHEZ & BABIN, 1993 (Famatina, western Argentina); *Pensarnia* COPE, 1996, and *Celtoconcha* COPE, 1996 (South Wales); *Dulcineaia* BABIN & GUTIÉRREZ-MARCO, 1991 (Spain); *Colpantyx* POJETA & GILBERT-TOMLINSON, 1977, and *Denticelox* POJETA & GILBERT-TOMLINSON, 1977 (Australia); *Haidongoconcha* FANG & COPE, 2004, and *Eopterinea* FANG & COPE, 2004 (eastern West Yunnan, Indochina); *Zadimerodia* GUO, 1988, and *Zhenxiongella* FANG & COPE, 2008 (eastern Yunnan, southern China).

The Ordovician diversification of bivalves is comparable to that of other animal classes: an extinction event (terminal Cambrian for bivalves) is followed by geographic dispersion from isolated populations, and then rapid evolutionary radiation. Through this process, anatomical and physiological novelties result in the origin of new life habits and clades. One example, among many, is the origin of epibenthic life habits in Ambonychiidae and other pteriomorphians, involving modification of shell outline, reduction of the anterior adductor muscle, and retention of a byssus in adults. In many cases, however, the new clade does not become widely dispersed, and it does not persist for long (e.g., *Lipanella*, *Synek*).

Paleogeographic reconstructions for the early Paleozoic indicate that the Gondwana core and a number of peripheral terrains extended over 100° paleolatitude, from the South Pole, then near North Africa, to the Equator. FORTEY and COCKS (2003) divided this supercontinent into three latitudinal belts: high latitude West Gondwana (North Africa, Armorica, Perunica, Avalonia), low latitude East Gondwana (mainly Australia and South China), and intermediate latitude Gondwana (mainly South America). The geographic distribution of Ordovician bivalve higher taxa seems to have been controlled largely by water temperature (COPE & BABIN, 1999; BABIN, 2001; COPE, 2002; FANG & COPE, 2004, 2008). Ordovician high-latitude bivalve faunas were dominated by heteroconchs, whereas low latitude faunas were dominated by pteriomorphians and nuculoids. The more temperate western Argentina shelves show a change in proportion of higher taxa, with heteroconchs dominating the NWA basin and pteriomorphians dominating the Famatina basin. SÁNCHEZ (2008) suggested that taxonomic differences between the two basins are due to the different tectonic setting, e.g., wide foreland siliciclastic platforms in the former and narrow volcaniclastic platforms in the latter. The lower latitude of Famatina with respect to NWA (ca. 10°) may account for the presence of pteriomorphians in Floian beds and their absence in NWA and Bolivia.

This initial diversification of bivalves during the Tremadocian and Floian was marked by three key features: adaptations for burrowing evolved in both Protobranchia and Autobranchia, feeding gills, and retention of the byssus in the adult stage (FANG, 2006a). The first feature allowed exploitation of previously unoccupied ecospace by means of pedal burrowing. It is likely that this was the main factor allowing for the initial radiation of protobranchs and, with some differences, also autobranchs (Fang, 2006a, 2006b). With only a few exceptions, Autobranchia were endofaunal during the early Ordovician, with the majority of its species then being shallow endofaunal. Although deeper burrowing was attained during the second Ordovician diversification, it seems likely that the NWA Dapingian genus *Konduria* Sánchez, 2007 (in Sánchez & Benedetto, 2007), which possessed a small pallial sinus and an elongate, low convexity shell, could have already been a relatively deep burrower (Sánchez & Benedetto, 2007). The cycloconchoid *Fasciculodonta* Fang and Cope, 2004, upper Floian–Dapingian, also has a shallow pallial sinus (Fang & Cope, 2004).

Feeding gills enhanced the diversification of autobranch but not protobranch bivalves during the Ordovician. Yonge (1947), Cope (1995, 1997, 2002, 2004), and Cope and Babin (1999) stressed the great importance of this feature in bivalve evolution. Feeding gills allowed some bivalves to ingest microorganisms and organic matter in suspension, thereby taking advantage of a nutrient source that increased with the advent of sea floor bioturbation. This adaptation can be inferred from the presence of strong hinge dentition in many Autobranchia. According to Cope (1995), suspension feeding requires the periodic voiding of rejected material (pseudofeces) from the gills by rapid opening and closing of the valves, and this, in turn, requires well-developed hinge teeth to keep the valves aligned. Pedal scars reduced in number and positioned high in the umbones in later Ordovician actinodonts may indicate enlargement of the mantle cavity, and therefore more efficient suspension feeding in that group (Morris, 1978). This suggests that the earlier actinodonts were poorly adapted for suspension feeding.

Byssal attachment, as Stanley (1975b) suggested, was a key feature for the diversification of Ordovician endobyssate taxa. The retention of the byssus in the adult stage allowed for fixation of the shell to the substrate, thereby enhancing stability in both endofaunal taxa, as well as in epifaunal taxa, in high energy environments. The presence of a byssus in the young and/or adult stages of Autobranchia (pteriomorphians and heteroconchs) suggests that it evolved before these two clades separated. This points to a pre-Ordovician common ancestor with at least a byssate larval stage. True byssal secretion is primitively absent in Protobranchia (Allen & Hannah, 1986; Bandel, 1988; Morton, 1995) and is therefore an apomorphy for autobranchs but not for the entire class Bivalvia (Waller, 1998). The significance of the evolution of a byssus in autobranchs has been stressed by Stanley (1972, 1977) and Morton (1995). The earliest record of an epifaunal life habit in bivalves is an undetermined, lower Floian ambonychiid from the Precordillera. The subsequent great diversification of ambonychiids in the late Ordovician is a reflection of the success of this structure.

In summary, the feeding gill and byssus are the major synapomorphies for Autobranchia, whereas detritus-collecting palp proboscides are the major autapomorphy for Protobranchia (Fang, 2006a).

The ability to form hinge teeth may be a synapomorphy for the Bivalvia. Although this may be true, bivalves show many examples of convergent return to an edentulous condition, thereby confounding attempts to use this feature as a primary basis for establishing higher level evolutionary relationships (Carter, Campbell, & Campbell, 2000). Cambrian *Fordilla* and *Pojetaia* were pretaxodont (Carter, Campbell, & Campbell, 2000), whereas modiolopsids, the earliest known Ordovician bivalves, were edentulous. Babin and Hammann (2001) and Babin (2002) suggested a hypothetical edentulous ancestor or having incipient cardinal and/or lateral teeth, which was neither taxodont nor actinodont. Dentate bivalves appeared in the Ordovician by the late Tremadocian, and by the early Floian, several dental patterns had appeared, e.g.,

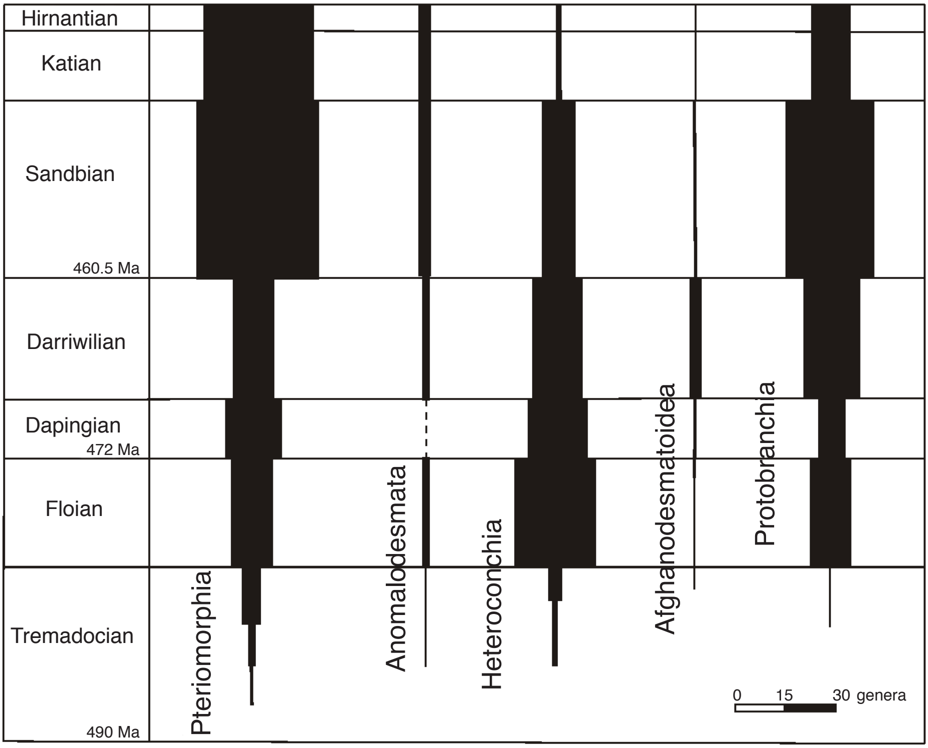


FIG. 5. Changing patterns of Ordovician bivalve diversity (adapted from Fang, 2006a).

different types of actinodonty (babinkids, redonids, cycloconchids), gradidentate paleotaxodonty (protobranchs), and heterotaxodonty (afghanodesmatids).

In the past, it has been customary to shoehorn some early Ordovician bivalves into higher taxa, for which they have some but not all of the diagnostic features. The ucumarids and *Arenigomya*, for example, display pustules at the intersection of commarginal and radial lines, and on this basis, they have been referred to Anomalodesmata. However, these taxa lack certain other features typical of extant Anomalodesmata. It may be best to define bivalve higher taxa polythetically, rather than on the basis of absolute apomorphies. In a polythetic higher taxon, members are required to posses only a specified majority of indicated apomorphies. In addition, some early taxa may be best classified as plesions, i.e., taxa close to but not fully members of a specified higher taxon.

LATE ORDOVICIAN RADIATION

The second Ordovician radiation of the Bivalvia occurred during Sandbian time and involved mostly pteriomorphians and protobranchs. At the same time, afghanodesmatoids (=cardiolarioids) and heteroconchs declined in diversity (Fig. 5). Bivalves expanded their distribution to Laurentia, Siberia, Baltica, and Kazakhstan, thereby becoming much more widespread. However, this radiation involved no new higher taxa. It is apparent only at the generic and familial levels. Colonization of extra-Gondwanan areas during the Sandbian may have been enhanced by a sea level highstand, as is well documented for Laurentia and Baltica (BABIN, 2001; NIELSEN, 2004).

Ambonychiids underwent an important late Ordovician radiation in Laurentia (POJETA, 1966, 1997). Most of the genera in this family are in fact confined to this paleocontinent. It has been postulated that this radiation was promoted by an input of terrigenous sediment from the Taconic orogeny (Miller & Mao, 1995).

Small radiation-extinction events have been recognized in some areas, as in the Sandbian of the Argentine Precordillera. The protobranchs there experienced a remarkable radiation (Sánchez, 1999b), which appears to be related to short-term oceanic warming (Sánchez, 1999a). This increase in temperature may also explain the occurrence of an undetermined ambonychiid in the upper Sandbian strata of the Precordillera terrain, which at that time was adjacent to Gondwana (Sánchez, 2003).

In summary, the late Ordovician bivalve radiation is characterized by the widespread colonization of mid- to low-latitude platforms and more restricted, local radiation events.

PROBABLE CAUSES OF THE TWO ORDOVICIAN EVOLUTIONARY RADIATIONS

The main difference between the two Ordovician radiation events is that the early Ordovician involved mainly new key features, such as pedal burrowing, feeding gills, and retention of the byssus in the adult, followed by the emergence of new adaptive strategies, whereas late Ordovician radiation involved an increase of genera and species within existing clades.

The early Ordovician radiation resulted in the appearance of all bivalve subclasses, superorders, and other principal clades, as well as the four major life habits, i.e., endobyssate filter-feeders (Modiolopsoidea, Cyrtodontoidea), free-burrowing deposit-feeders (Protobranchia), free-burrowing filter-feeders (Heteroconchia), and epibyssate filter-feeders (Pterineidae) (Fang, 2006a). Siphons were a common feature in unrelated, burrowing lineages, but siphonate burrowing did not become fully established until the Devonian (Stanley, 1977). Siphons can be recognized in fossils by the presence of a posterior pallial sinus. They allowed deeper infaunal colonization, an important advantage in the face of increasing predation (Vermeij, 1987). However, this feature was restricted to a few Ordovician genera (e.g., *Konduria*, *Fasciculodonta*, and *Lyrodesma* Conrad, 1841) and was not an important factor for the late Ordovician radiation.

A comparable late Ordovician increase in diversity was attained by other invertebrate taxa, such as echinoderms, gastropods, and brachiopods (Webby & others, 2004). It followed an interval of evolutionary stasis, spanning broadly Darriwilian time, when bivalves were still geographically restricted to peri-Gondwanan shelf areas. It was not until the latest middle Ordovician that bivalves began to escape the confines of Gondwana, thereby triggering the late Ordovician radiation (Fang, 2006a).

In summary, modern-type bivalves originated in the Ordovician (Miller, 1990), with all principal clades and all four principal life-habit groups initially appearing during the early Ordovician. Bivalves therefore accomplished major morphological innovations relatively rapidly during the Cambrian–Ordovician transition. The most remarkable phenomenon is the nearly simultaneous appearance of these innovations. This is consistent with the general pattern in other invertebrate groups, where major morphological innovations occur primarily during their early history, and subsequent evolution involves elaboration and variation on these themes (Stanley, 1968; Mayr, 1982b; Erwin, 1994). The basal dichotomy between protobranchs and autobranchs and the basal branching among autobranchs must have been completed during this early period.

REFERENCES

Allen, J. A. 1978. Evolution of the deep sea protobranch bivalves. Philosophical Transactions of the Royal Society of London (series B) 284:387–401.

Allen, J. A. 1985. The Recent Bivalvia: Their form and evolution. *In* E. R. Trueman. & M. R. Clarke, eds., The Mollusca, 10, Evolution. Academic Press. Orlando, Florida. p. 337–403.

Allen, J. A., & F. J. Hannah. 1986. A reclassification of the Recent genera of the subclass Protobranchia (Mollusca: Bivalvia). Journal of Conchology 32(4):225–249.

Arthur, W. 2002. The emerging conceptual framework of evolutionary developmental biology. Nature 415:757–764.

Astini, R. A. 2003. The Ordovician proto-Andean basins. *In* J. L. Benedetto, ed., Ordovician fossils of Argentina. Secretaría de Ciencia y Tecnología. Universidad Nacional de Córdoba. Córdoba. p. 1–74.

Babin, C. 1966. Mollusques bivalves et céphalopods du Paléozoïque armoricain. Etude systematique. Essai sur la phylogénie des Bivalves. Esquisse paléoécologique. Imprimerie Commerciale et Administrative. Brest. p. 1–471.

Babin, C. 1982. Mollusques bivalves et rostroconches. *In* C. Babin, R. Courtessole, M. Melou, J. Pillet, D. Vizcaino, & E. Yochelson, eds., Brachiopodes (Articulés) et Mollusques (Bivalves, Rostroconches, Monoplacophores, Gastropodes) de l'Ordovicien Inférieur (Trémadocien-Arenigien) de la Montagne Noire (Frnce Méridionale). Mémoire de la Societé d'Etudes Scientifiques de l'Aude. Carcassonne. p. 1–63.

Babin, C. 1993. Rôle des plates-formes gondwaniennes dans les diversifications des mollusques bivalves durant l'Ordovicien. Bulletin de la Société géologique de France 164:141–153.

Babin, C. 1995. The initial Ordovician bivalve molllusk radiations on the western Gondwanan shelves. *In* J. D. Cooper, M. L. Droser, & S. C. Finney, eds., Ordovician Odyssey, Short Papers for the 7th International Symposium on the Ordovician System, California. The Pacific Section of the Society for Sedimentary Geology (SEPM), Fullerton 77:491–498.

Babin, C. 2001. Ordovician to Devonian diversification of the Bivalvia. American Malacological Bulletin 15(2):167–178.

Babin, C. 2002. Les mollusques bivalves primitifs: L'enquête paléontologique. Haliotis 31:3–12.

Babin, C., & J. C. Gutiérrez-Marco. 1991. Middle Ordovician bivalves from Spain and their phyletic and palaeogeographic significance. Palaeontology 34:109–147.

Babin, C., & W. Hammann. 2001. Une nouvelle espèce de *Modiolopsis* (Bivalvia) dans l'Arenig (Ordovicien Inférieur) de Daroca (Aragon, Espagne): Réflexions sur la denture des bivalves primitifs. Revista Española de Paleontología 16:269–282.

Bandel, K. 1988. Stages in the ontogeny and a model of the evolution of bivalves (Mollusca). Paläontologische Zeitschrift 62:217–254.

Barrande, J. 1881. Système Silurien du Centre de la Bohême, Classe des Mollusques, Ordre des Acéphalés, vol. 6. Chez l'auteur et éditeur. Prague, Paris. p. 1–342.

Baratte, S., A. Andouche, & L. Bonnaud. 2007. *Engrailed* in cephalopods: A key gene related to the emergence of morphological novelties. Development Genes and Evolution 217:353–362.

Benedetto, J. L. 2003. Paleobiogeography. *In* J. L. Benedetto, ed., Ordovician fossils of Argentina. Secretaría de Ciencia y Tecnología. Universidad Nacional de Córdoba. Córdoba. p. 91–110.

Benedetto, J. L. 2004. The allochthony of the Argentine Precordillera ten years later (1993–2003): A new paleobiogeographic test of the microcontinental model. Gondwana Research 7:1027–1039.

Benedetto, J. L., T. M. Sánchez, M. G. Carrera, E. D. Brussa, & M. J. Salas. 1999. Paleontological constraints on successive paleogeographic positions of Precordillera terrain during the early Paleozoic. *In* V. Ramos & D. Keppie, eds., Gondwana-Laurentia connections before Pangea. Geological Society of America, Special Paper 336:21–42.

Bottjer, D. J., J. W. Hagadorn, & S. Q. Dornbos. 2000. The Cambrian substrate revolution. GSA Today 10(9):1–7.

Budd, G. E., & S. R. Jensen. 2000. A critical reappraisal of the fossil record of the bilaterian phyla. Biological Review 75:253–295.

Caron, J.-B., A. Scheltema, C. Schander, & D. Rudkin. 2006. A soft-bodied mollusc with radula from the Middle Cambrian Burgess Shale. Nature 442:159–163.

Carter, J. G. 2001. Shell and ligament microstructure of selected Silurian and Recent palaeotaxodonts (Mollusca: Bivalvia). American Malacological Bulletin 16:217–238.

Carter, J. G. 2011. Eubivalvia Carter. *In* Joseph G. Carter, Cristian R. Altaba, Laurie C. Anderson, Rafael Araujo, Alexander S. Biakov, Arthur E. Bogan, David C. Campbell, Matthew Campbell, Chen Jinhua, John C. W. Cope, Graciela Delvene, Henk H. Dijkstra, Fang Zong-jie, Ronald N. Gardner, Vera A. Gavrilova, Irina A. Goncharova, Peter J. Harries, Joseph H. Hartman, Michael Hautmann, Walter R. Hoeh, Jorgen Hylleberg, Jiang Bao-yu, Paul Johnston, Lisa Kirkendale, Karl Kleemann, Jens Koppka, Jiří Křĭž, Deusana Machado, Nikolaus Malchus, Ana Márquez-Aliaga, Jean-Pierre Masse, Christopher A. McRoberts, Peter U. Middelfart, Simon Mitchell, Lidiya A. Nevesskaja, Sacit Özer, John Pojeta, Jr., Inga V. Polubotko, Jose Maria Pons, Sergey Popov, Teresa Sánchez, André F. Sartori, Robert W. Scott, Irina I. Sey, Javier H. Signorelli, Vladimir V. Silantiev, Peter W. Skelton, Thomas Steuber, J. Bruce Waterhouse, G. Lynn Wingard, & Thomas Yancey, eds. A Synoptical Classification of the Bivalvia (Mollusca). The University of Kansas Paleontological Contributions 4:20.

Carter, J. G., D. C. Campbell, & M. R. Campbell. 2000. Cladistic perspectives on early bivalve evolution. *In* E. M. Harper, J. D. Taylor, & J. A. Crame, eds., The Evolutionary Biology of the Bivalvia. Geological Society of London, Special Publication 177:47–79.

Chaparro, O. R., J. A. Videla, & R. J. Thompson. 2001. Gill morphogenesis in the oyster *Ostrea chilensis*. Marine Biology 138:199–207.

Conrad, T. A. 1841. Fifth annual report on the palaeontology of the strata of New York. Geological Survey 5:25–57.

Cope, J. C. W. 1995. The early evolution of the Bivalvia. *In* J. D. Taylor, ed., Origin and Evolutionary Radiation of the Mollusca. Oxford University Press. Oxford. p. 361–370.

Cope, J. C. W. 1996. Early Ordovician (Arenig) bivalves from the Llangynog Inlier, South Wales. Palaeontology 39:979–1025.

Cope, J. C. W. 1997. The early phylogeny of the class Bivalvia. Palaeontology 40:713–746.

Cope, J. C. W. 2002. Diversification and biogeography of bivalves during the Ordovician Period. *In* J. A. Crame & A. W. Owen, eds., Palaeobiogeography and Biodiversity Change: A Comparison of the Ordovician and Mesozoic–Cenozoic Radiations. Geological Society, London, Special Publications 194:35–52.

Cope, J. C. W. 2004. Bivalve and Rostroconch mollusks. *In* B. D. Webby, F. Paris, M. L. Droser, & I. G. Percival, eds., The Great Ordovician Biodiversification Event. Columbia University Press. New York. p. 196–208.

Cope, J. C. W., & C. Babin. 1999. Diversification of bivalves in the Ordovician. Geobios 32:175–185.

Cox, Leslie R., C. P. Nuttall, & E. R. Trueman. 1969. General features of Bivalvia. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology, Part N, Mollusca 6, Bivalvia, vol. 1–2. Geological Society of America & University of Kansas. Boulder & Lawrence. p. 2–129.

Dornbos, S. Q., D. J. Bottjer, & Chen J.-Y. 2004. Evidence for seafloor microbial mats and associated metazoan lifestyles in lower Cambrian phosphorites of Southwest China. Lethaia 37:127–137.

Erwin, D. H. 1994. Early introduction of major morphological innovatons. Acta Palaeontologica Polonica 38:281–294.

Fang Zong-jie. 2006a. An introduction to Ordovician bivalves of southern China, with a discussion of the early evolution of the Bivalvia. Geological Journal 41:303–328.

Fang Zong-jie. 2006b. A new scenario for the early evolution of the Bivalvia. *In* N. Malchus & J. M. Pons, eds., Abstracts and Posters of the International Congress on Bivalvia at the Universitat Autonoma de Barcelona, Spain, 22–27 July 2006. Organisms Diversity & Evolution, 6, Electronic Supplement 16(1):30–31.

Fang Zong-jie. 2006c. Ordovician bivalve radiation in southern China, with a discussion on the cause of difersification. *In* Rong Jia-yu, Fang Zong-jie, Zhou Zhong-he, Zhan Ren-bin, Wang Xiang-dong, & Yuan Xun-lai, eds., Originations, Radiations and Biodiversity Changes—Evidences from the Chinese Fossil Record. Beijing. Science Press. p. 215–258. In Chinese, with English summary on p. 861–863.

Fang Zong-jie, & J. C. W. Cope. 2004. Early Ordovician bivalves from Dali, West Yunnan, China. Palaeontology 47(5):1121–1158.

Fang Zong-jie, & J. C. W. Cope. 2008. Affinities and palaeobiogeographical significance of some Ordovician bivalves from East Yunnan, China. Alcheringa 32:297–312.

Fortey, R. A., & L. R. M. Cocks. 2003. Palaeontological evidence bearing on global Ordovician-Silurian continental reconstructions. Earth-Science Reviews 61:245–307.

Fuchs, A. 1919. Beitrag zur Kenntnis der Devonfauna der Verse- und der Hobräcker Schichten des Sauerländischen Faciesgebietes. Jahrbuch der Preussischen geologischen Landesanstalt (1918) 39:58–95.

Gatenby, C. M., B. C. Parker, & R. J. Neves. 1997. Growth and survival of juvenile rainbow mussels, *Villosa iris* (Lea, 1829) (Bivalvia: Unionidae), reared on algal diets and sediment. American Malacological Bulletin 14(1):57–66.

Geyer, G., & M. Streng. 1998. Middle Cambrian pelecypods from the Anti-Atlas, Morocco. Revista Espanola de Paleontologia, Homenaje al Prof. Gonzalo Vidal, Numero Extra, p. 83–96.

Gibert, J.-M. 2002. The evolution of *engrailed* genes after duplication and speciation events. Development Genes and Evolution 212:307–318.

Giribet, G., A. Okusu, A. R. Lindgren, S. W. Huff, M. Schrödl, & M. K. Nishiguchi. 2006. Evidence for a clade composed of molluscs with serially repeated structures: Monoplacophorans are related to chitons. Proceedings of the National Academy of Sciences, USA 103:7723–7728.

Giribet, G., & W. Wheeler. 2002. On bivalve phylogeny: A high-level analysis of the Bivalvia (Mollusca) based on combined morphology and DNA sequence data. Invertebrate Biology 121(4):271–324.

Gmelin, J. F. 1791 [1790]. Vermes. Tome I, Pars VI. *In* Caroli A. Linné & J. F. Gmelin, eds., 1788–1793, Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Editio Decima Tertia [13th edit.], Aucta, Reformata, 3 vol. Georg. Emanuel Beer. Lipsiae. 2 + p. 3021–3910.

Grabau, A. W. 1900. Palaeontology of the Cambrian terranes of the Boston Basin. Occasional Papers of the Boston Society of Natural History 4:601–694.

Guo Fu-xiang. 1988. New genera of fossil bivalves from Yunnan. Yunnan Geology 7:112–144. In Chinese with English abstract.

Hall, J. 1847. Natural History of New York. Paleontology of New York, vol. 1. Containing Descriptions of the Organic remains of the Lower Division of the New York System (Equivalent of the Lower Silurian Rocks of Europe). Van Benthuysen. Albany. xxiii + 339 p.

Harper, D. A., L. R. M. Cocks, L. E. Popov, P. M. Sheehan, M. G. Bassett, P. Copper, L. E. Holmer, Jin Ju-gan, & Rong Jia-yu. 2004. Brachiopods. *In* B. D. Webby, F. Paris, M. L. Droser, & I. G. Percival, eds., The Great Ordovician Biodiversification Event. Columbia University Press. New York. p. 157–178.

Haszprunar, G. 2000. Is the *Aplacophora* monophyletic? A cladistic point of view. American Malacological Bulletin 15:115–130.

Hinz-Schallreuter, I. 1995. Muscheln (Pelecypoda) aus dem Mittelkambrium von Bornholm. Geschiebekunde Aktuell 11(3):71–84.

Hinz-Schallreuter, I. 2000. Middle Cambrian Bivalvia from Bornholm and a review of Cambrian bivalved Mollusca. Revista Española de Micropaleontología 32(2):225–242.

Hsu Singwu, & Ma C. T. 1948. The I-Chang Formation and the Ichangian fauna. Contributions from the National Research Institute of Geology, Academia Sinica 8:1–51.

Iijima, M., N. Akiba, I. Sarashina, S. Kuratani, & K. Endo. 2006. Evolution of Hox genes in molluscs: A comparison among seven morphologically diverse classes. Journal of Molluscan Studies 72:259–266.

Iijima, M., T. Takeuchi, I. Sarashina, & K. Endo. 2008. Expression patterns of *engrailed* and *dpp* in the gastropod *Lymnaea stagnalis*. Development Genes and Evolution 218:237–251.

Isberg, O. 1934. Studien über Lamellibranchiaten des Leptaenakalkes in Dalarna. Hakan Ohlssons Buchdruckerei. Lund. p. 1–422.

Jacobs, D. K., C. G. Wray, C. J. Wedeen, R. Kostriken, R. DeSalle, J. L. Staton, R. D. Gates, & D. R. Lindberg. 2000. Molluscan *engrailed* expression, serial organization and shell evolution. Evolution and Development 2:340–347.

Jell, P. A. 1980. Earliest known pelecypod on earth—A new early Cambrian genus from South Australia. Alcheringa 4:233–239.

Kin, K., S. Kakoi, & H. Wada. 2009. A novel role for *dpp* in the shaping of bivalve shells revealed in a conserved molluscan developmental program. Developmental Biology 329:152–166.

Kniprath, E. 1981. Ontogeny of the molluscan shell field: A review. Zoologica Scripta 10:61–79.

Kouchinsky, A. V. 1999. Shell microstructures of the Early Cambrian *Anabarella* and *Watsonella* as new evidence on the origin of the Rostroconchia. Lethaia 32:173–180.

Kouchinsky, A. V. 2000. Shell microstructure in early Cambrian mollusks. Acta Palaeontologica Polonica 45(2):119–150.

Lea, I. 1829. Description of a new genus of the family of naiades, including eight new species, four of which are new; also the description of eleven new species of the genus *Unio* from the rivers of the United States: With observations on some of the characters of the naiades. Transactions of the American Philosophical Society (new series) 3:403–457.

Levinton, J. S., J. E. Ward, & R. J. Thompson. 1996. Biodynamics of particle processing in bivalve molluscs: Models, data, and future directions. Invertebrate Biology 115:232–242.

MacKinnon, D. I. 1982. *Tuarangia paparua*, n. gen. and n. sp., a late Middle Cambrian pelecypod from New Zealand. Journal of Paleontology 56(3):589–598.

MacKinnon, D. I. 1985. New Zealand late Middle Cambrian mollusks and the origin of Rostroconchia and Bivalvia. Alcheringa 9:65–81.

Mayr, E. 1942. Systematics and the Origin of Species. Columbia University Press. New York. p. 1–330.

Mayr, E. 1954. Change of genetic environment and evolution. *In* J. Huxley, A .C. Hardy, & E. B. Ford, eds., Evolution as a Process. Allen and Unwin. London. p. 157–180.

Mayr, E. 1963. Animal Species and Evolution. Harvard University Press. Cambridge. p. 1–811.

Mayr, E. 1982a. Processes of speciation in animals. *In* D. Barigozzi, ed., Mechanisms of Speciation. Alen R Liss, Inc. New York. p. 1–19.

Mayr, E. 1982b. The Growth of Biological Thought. The Belknap Press of Harvard University Press. Cambridge. p. 1–992.

Miller, A. I. 1988. Spatio-temporal transitions in Paleozoic Bivalvia; an analysis of North American fossil assemblages. Historical Biology 1:251–273.

Miller, A. I. 1990. Bivalves. *In* K. J. McNamara, ed., Evolutionary Trends. Belhaven Press. London. p. 143–161.

Miller, A. I., & S. Mao. 1995. Association of orogenic activity with the Ordovician radiation of marine life. Geology 23:305–308.

Morris, N. J. 1978. The infaunal descendants of the Cycloconchidae: An outline of the evolutionary history and taxonomy of the Heteroconchia, superfamilies Cycloconchacea to Chamacea. Philosophical Transactions Royal Society, London (series B) 284:259–275.

Morris, N. J. 1979. On the origin of the Bivalvia. *In* M. R. House, ed., The Origin of Major Invertebrate Groups. Systematics Association Special Volume 12:381–413.

Morris, N. J. 1980. A new Lower Ordovician bivalve family, the Thoraliidae (?Nuculoida), interpreted as actinodont deposit feeders. Bulletin of the British Museum of Natural History (Geology) 34:265–272.

Morris, N. J. 1990. Early radiations of the Mollusca. *In* J. D. Taylor & G. P. Larwood, eds., Major Evolutionary Radiations. The Systematics Association Special Volume 42:73–90.

Morris, N. J., & R. A. Fortey. 1976. The significance of *Tironucula* gen. nov. to the study of bivalve evolution. Journal of Paleontology 50:701–709.

Morton, B. 1995. The evolutionary history of the Bivalvia. *In* J. D. Taylor, ed., Origin and Evolutionary Radiation of the Mollusca. Oxford University Press. Oxford. p. 337–359.

Moshel, S. M., M. Levine, & J. R. Collier. 1998. Shell differentiation and *engrailed* expression in the *Ilyanassa* embryo. Development Genes and Evolution 208:135–141.

Nederbragt, A. J., A. E. van Loon, & W. Dictus. 2002. Expression of *Patella vulgata* orthologs of *engrailed* and *dpp-BMP2/4* in adjacent domains during molluscan shell development suggests a conserved compartment boundary mechanism. Developmental Biology 246:341–355.

Nevesskaja, Lidiya A. 2009. Principles of systematics and the system of bivalves. Paleontologicheskii Zhurnal 1:3–13. In Russian; see also English translation in Paleontological Journal, 2009.

Nielsen, A. T. 2004. Ordovician sea level Changes: A Baltoscandian perspective. *In* B. D. Webby, F. Paris, M. L. Droser, & I. G. Percival, eds., The Great Ordovician Biodiversification Event. Columbia University Press. New York. p. 84–93.

Novak-Gottshall, P. M., & A. I. Miller. 2003. Comparative geographic and environmental diversity dynamics of grastropods and bivalves during the Ordovician Radiation. Paleobiology 29:576–604.

O'Beirn, F. X., R. J. Neves, & M. B. Steg. 1998. Survival and growth of juvenile freshwater mussels (Unionidae) in a recirculating aquaculture system. American Malacological Bulletin 14(2):165–171.

Passamaneck, Y. J., C. Schander, & K. M. Halanych. 2004. Investigation of molluscan phylogeny using large-subunit and small-subunit nuclear rRNA sequences. Molecular Phylogenetics and Evolution 32(2004):25–38.

Pojeta, Jr., J. 1966. North American Ambonychiidae (Pelecypoda). Palaeontographica Americana 5(36):132–241.

Pojeta, Jr., J. 1987. Class Pelecypoda. *In* R. S. Boardman, A. H. Cheetham, & A. J. Rowell, eds., Fossil

Invertebrates. Blackwell Scientific Publications. Boston. p. 386–435.

Pojeta, Jr., J. 1997. *Claudeonychia babini* nov. gen. et nov. sp. of Ordovician ambonychiid pelecypods from Cincinnati, Ohio, USA. Geobios Memoir Series 20:433–436.

Pojeta, Jr., J. 2001. Cambrian Pelecypoda (Mollusca). American Malacological Bulletin 15(2):157–166.

Pojeta, Jr., J., & J. Gilbert-Tomlinson. 1977. Australian Ordovician pelecypod molluscs. Bureau of Mineral Resources, Geology and Geophysics Bulletin 174:1–64.

Pojeta, Jr., J., & B. Runnegar. 1976. The paleontology of rostroconch mollusks and the early history of pelecypod mollusks. United States Geological Survey Professional Paper 968:1–88.

Pojeta, Jr., J., & B. Runnegar. 1985. The early evolution of diasome molluscs. *In* E. R. Trueman & M. R. Clarke, eds., The Mollusca, 10, Evolution. Academic Press. Orlando. p. 295–336.

Purchon, R. D. 1978. An analytical approach to a classification of the Bivalvia. Philosophical Transactions of the Royal Society of London (series B) 284:425–436.

Reid, R. G. B., & D. G. Brand. 1986. Sulfide-oxidizing symbiosis in lucinaceans: Implications for bivalve evolution. The Veliger 29:3–24.

Reid, R. G. B., R. F. McMahon, D. Ó. Foighil, & R. Finnigan. 1992. Anterior inhalant currents and pedal feeding in bivalves. The Veliger 35(2):93–104.

Rouault, M. 1851. Mémoires sur le terrain paleozoïque des environs de Rennes. Bulletin de la Société géologique de France (series 2) 8:358–399.

Runnegar, B. 1983. Molluscan phylogeny revisited. Memoir of Association of Australasian Palaeontologists 1:121–144.

Runnegar, B. 1996. Early evolution of the Mollusca: The fossil record. *In* J. D. Taylor, ed., Origin and Evolutionary Radiation of the Mollusca. Oxford University Press. Oxford. p. 77–87.

Runnegar, B., & C. Bentley. 1983. Anatomy, ecology, and affinities of the Australian Early Cambrian bivalve *Pojetaia runnegari* Jell. Journal of Paleontology 57(1):73–92.

Runnegar, B., & J. Pojeta, Jr. 1974. Molluscan phylogeny: The paleontological viewpoint. Science 186:311–317.

Runnegar, B., & J. Pojeta, Jr. 1976. The paleontology of rostroconch mollusks and the early history of the phylum Mollusca. U. S. Geological Survey Professional Paper 968:1–88.

Runnegar, B., & J. Pojeta, Jr. 1985. Origin and diversification of the Mollusca. *In* E. R. Trueman & M. R. Clarke, eds., The Mollusca, 10, Evolution. Academic Press. Orlando. p. 1–57.

Runnegar, B., & J. Pojeta, Jr. 1992. The earliest bivalves and their Ordovician descendants. American Malacological Bulletin 9(2):117–122.

Salvini-Plawen, L. v. 1985. Early evolution and the primitive groups. *In* E. R. Trueman & M. R. Clarke, eds., The Mollusca, 10, Evolution. Academic Press. Orlando. p. 59–150.

Sánchez, T. M. 1999a. Caradoc bivalves from the Argentine Precordillera: A local radiation extinction event. Geobios 32:333–340.

Sánchez, T. M. 1999b. New late Ordovician (early Caradoc) bivalves from the Sierra de Villicum (Argentine Precordillera). Journal of Paleontology 73:66–76.

Sánchez, T. M. 2001. Bivalvia (Mollusca) de la Formación San Juan (Ordovícico temprano, Precordillera Argentina). Ameghiniana 38(4):471–475.

Sánchez, T. M. 2003. Chapter 8. Bivalvia and Rostroconchia. *In* J. L. Benedetto, ed., Ordovician fossils of Argentina. Secretaría de Ciencia y Tecnología, Universidad Nacional de Córdoba. Córdoba. p. 273–293.

Sánchez, T. M. 2005. New Bivalvia and Rostroconchia from the Early Ordovician (Late Tremadoc–Middle Arenig) of northwestern Argentina. Journal of Paleontology 79:532–541.

Sánchez, T. M. 2006. Taxonomic position and phylogenetic relationships of the bivalve *Goniophorina* Isberg and related genera from the Early Ordovician of northwestern Argentina. Ameghiniana 43:113–122.

Sánchez, T. M. 2007. Ecological-taxonomic levels in bivalve evolution and the Ordovician radiation. Acta Paleontologica Sinica 46:440–444.

Sánchez, T. M. 2008. The early bivalve radiation in the Ordovician Gondwanan basins of Argentina. Alcheringa 32:223–246.

Sánchez, T. M., & C. Babin. 1993. Un insolite mollusque bivalve, *Catamarcaia* n. g., de l'Arnig (Ordovicien inférieur) d'Argentine. Comptes Rendus de l'Académie des Sciences, Paris (série II) 316:265–271.

Sánchez, T. M., & J. L. Benedetto. 2007. The earliest estuarine bivalve assemblage, Lower Ordovician (Arenig) of northwestern Argentina. Geobios 40:523–533.

Sánchez, T. M., & N. E. Vaccari. 2003. Ucumariidae new family (Bivalvia, Anomalodesmata) and other bivalves from the Early Ordovician (Tremadocian) of northwestern Argentina. Ameghiniana 40(3):415–424.

Seilacher, A. 1999. Biomat-related lifestyles in the Precambrian. PALAIOS 14:86–93.

Seilacher, A., L. A. Buatois, & L. G. Màngano. 2005. Trace fossils in the Ediacaran-Cambrian transition: Behavioral diversification, ecological turnover and environmental shift. Palaeogeography, Palaeoclimatology, Palaeoecology 227:323–356.

Stanley, S. M. 1968. Post-Paleozoic adaptive radiation of infaunal bivalve molluscs—A consequence of mantle fusion and siphon formation. Journal of Paleontology 42:214–229.

Stanley, S. M. 1970. Relation of the shell form to life habits of the Bivalvia (Mollusca). Memoirs of the Geological Society of America 125:1–296.

Stanley, S. M. 1972. Functional morphology and evolution of byssally attached bivalve mollusks. Journal of Paleontology 46:165–212.

Stanley, S. M. 1975a. Why clams have the shape they have: An experimental analysis of burrowing. Paleobiology 1(1):48–58.

Stanley, S. M. 1975b. Adaptive themes in the evolution of the Bivalvia (Mollusca). Annual Review of Earth and Planetary Sciences 3:361–385.

Stanley, S. M. 1977. Trends, rates, and patterns of evolution in the Bivalvia. *In* A. Hallam, ed., Patterns of Evolution as Illustrated by the Fossil Record. Elsevier. Amsterdam. p. 209–250.

Stasek, C. R. 1961. The ciliation and function of the labial palps of *Acila castrensis* (Protobranchia, Nuculidae) with an evaluation of the role of the protobranch organs of feeding in the evolution of the Bivalvia. Proceedings of the Zoological Society of London 137:511–538.

Stasek, C. R. 1963. Synopsis and discussion of the association of ctenial and labial palps in the bivalved Mollusca. The Veliger 6:91–97.

Stasek, C. R. 1965. Feeding and particle sorting in *Yoldia ensifera* (Bivalvia: Protobranchia), with notes on other nuculanids. Malacologia 2:349–366.

Stead, R. A., R. J. Thompson, & J. R. Jaramillo. 2003. Absorption efficiency, ingestion rate, gut passage time and scope for growth in suspension- and deposit-feeding *Yoldia hyperborea*. Marine Ecology Progress Series 252:159–172.

Tevesz, M. J. S., & P. L. McCall. 1976. Primitive life habits and adaptative significance of the pelecypod form. Paleobiology 2(3):183–190.

Tevesz, M. J. S., & P. L. McCall. 1985. Primitive life habits of Bivalvia reconsidered. Journal of Paleontology 59(5):1326–1330.

Tomlin, J. R. le B. 1931. Some preoccupied generic names. Proceedings of the Malacological Society London 19:174–175.

Torigoe, K., & A. Inaba. 1981. On the scientific name of Japanese spiny oyster 'Kegaki.' Venus 40:126–134.

Trueman, E. R. 1966. Bivalve mollusks: Fluid dynamics of burrowings. Science 152:523–525.

Ushatinskaya, G. T. 2001. Brachiopods. *In* A. Yu. Zhuravlev & R. Riding, eds., The Ecology of the Cambrian Radiation. Columbia University Press. New York. p. 350–369.

Valentine, J. W., D. H. Erwin, & D. Jablonski. 1996. Developmental evolution of metazoan body plans: The fossil evidence. Developmental Biology 173:373–381.

Veniot, A., V. M. Bricelj, & P. G. Beninger. 2003. Ontogenetic changes in gill morphology and potential significance for food acquisition in the scallop *Placopecten magellanicus*. Marine Biology 142:123–131.

Vermeij, G. J. 1987. Evolution and Escalation: An Ecological History of Life. Princeton University Press. Princeton. xvi + p. 1–527.

Vogel, K. 1962. Muscheln mit Schlosszähnen aus dem spanischen Kambrium und ihre Bedeutung für die Evolution der Lamellibranchiaten. Akademie der Wissenschaften und der Literatur, Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse, Mainz 1962(4):192–244.

Vogel, K., & W. F. Gutmann. 1980. The derivation of pelecypods: Role of biomechanics, physiology and environment. Lethaia 13(3):269–275.

Vostokova, V. A. 1962. Cambrian gastropods of the Siberian Platform and Taymyr. Collection of Papers on Paleontology and Biostratigraphy [Sbornik statei po paleontologii i biostratigrafii]. Trudy Nauchnogo Issledovatelskogo Instituta Geologii Arktiki 28:51–74. In Russian.

Waller, T. R. 1981. Functional morphology and development of veliger larvae of the European Oyster, *Ostrea edulis* L. Smithsonian Contributions to Zoology 328:1–70.

Waller, T. R. 1990. The evolution of ligament systems in the Bivalvia. *In* B. Morton, ed., The Bivalvia—Proceedings of a Memorial Symposium in Honour of Sir Charles Maurice Yonge, Edinburg, 1986. Hong Kong University Press. Hong Kong. p. 49–71.

Waller, T. R. 1998. Origin of the molluscan class Bivalvia and the phylogeny of major groups. *In* P. A. Johnston & J. W. Haggart, eds., Bivalves: An Eon of Evolution—Paleobiological Studies Honoring Norman D. Newell. University of Calgary Press. Calgary. p. 1–45.

Wanninger, A., & G. Haszprunar. 2001. The expression of an *engrailed* protein during embryonic shell formation of the tusk-shell, *Antalis entalis* (Mollusca, Scaphopoda). Evolution and Development 3:312–321.

Webby, B. D., F. Paris, M. Droser, & I. G. Percival, eds. 2004. The Great Ordovician Biodiversification Event. Columbia University Press. New York. p. 1–484.

Wright, A. D. 1979. Brachiopod radiation. *In* M. R. House, ed., The Origin of Major Invertebrate Groups. Systematics Association Special Volume 12:235–252.

Yeager, M. M., D. S. Cherry, & R. J. Neves. 1994. Feeding and burrowing behaviors of juvenile rainbow mussels, *Villosa iris* (Bivalvia: Unionidae). Journal of the North American Benthological Society 13(2):217–222.

Yonge, C. M. 1939. The probranchiate Mollusca: A functional interpretation of their structure and evolution. Philosophical Transactions of the Royal Society of London (series B) 230:79–147.

Yonge, C. M. 1947. The pallial organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca. Philosophical Transactions of the Royal Society of London (series B) 232:443–518.

Yonge, C. M. 1978. Significance of the ligament in the classification of the Bivalvia. Proceedings of the Royal Society of London (series B) 202:231–248.

Yonge, C. M. 1983. Symmetries and the role of the mantle margins in the bivalve Mollusca. Malacological Review 16:1–10.

Zhang Zhifei, Shu Degan, Han Jian, & Liu Jianni. 2005. Morpho-anatomical differences of the Early Cambrian Chengjiang and Recent lingulids and their implications. Acta Zoologica (Stockholm) 86:277–288.

Zhuravlev, A. Y. 2001. Biotic diversity and structure during the Neoproterozoic-Ordovician transition. *In* A. Y. Zhuravlev & R. Zhuravlev, eds., The Ecology of the Cambrian Radiation. Columbia University Press. New York. p. 173–199.